LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *GOEDENIA SETOSA* (FOOTE) (DIPTERA: TEPHRITIDAE) ON *ERICAMERIA BRACHYLEPIS* (A. GRAY) H. M. HALL IN SOUTHERN CALIFORNIA

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Abstract.—*Goedenia setosa* (Foote) is a rare, monophagous or nearly monophagous, univoltine fruit fly (Diptera: Tephritidae) that feeds in the flower heads of *Ericameria brachylepis* (A. Gray) H. M. Hall in southern California. This sole, newly reported host belongs to the family Asteraceae tribe, Astereae, and subtribe Solidagininae, like all other known hosts of *Goedenia* spp. The third-instar larvae and puparia are described and figured, and selected characteristics of these stages are compared with the same stages of two other species of *Goedenia*. The prothorax and gnathocephalon of the second and third instars are smooth and mostly free of the minute acanthae that circumscribe most other body segments. The third instar of *G. setosa* lacks oral ridges, as do the third instars of two other congeners studied to date. The anterior thoracic spiracle bears two papillae in the third instar. Minute acanthae cover the center of the posterior end of the truncated, posteriorly sclerotized, caudal segment, that also is perforated by scattered, open pores, and this central area is ringed by concentric series of shallow, elliptical depressions. The life cycle is of the aggregative type. Overwintering limitedly occurs as sexually immature adults, but more frequently in dead flower heads as prepuparial third instars and puparia in apically open, vasiform cells consisting of floret and achene fragments impregnated and hardened with dried liquid feces and sap. The flattened, sclerotized posterior of the caudal segment of the overwintering prepuparium serves to plug the apical opening of the cell and thus possibly helps to shield it at least from predators. However, *Colotrechnus* sp. (Eulophidae), *Eurytoma* sp. (Eurytomidae), *Eupelmus* sp. (Eupelmidae), *Halticoptera* (Pteromalidae), and *Mesopolobus* sp. (Pteromalidae) are chalcidoid, primary parasitic Hymenoptera commonly reared from the overwintered puparia.

Key Words: Insecta, *Goedenia, Ericameria,* Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, aggregative life cycle, seed predation, parasitoids

Indigenous, western North American Myopitini (Diptera: Tephritidae: Tephritinae) formerly assigned to the Palearctic genus *Urophora* Robineau-Desvoidy were redesignated as *Goedenia* by Freidberg and Norrbom (1999). To date, the life history and immature stages of two of the eight known species of *Goedenia* have been described in detail, i.e., *G. timberlakei* (Blanc and Foote) and *G. rufipes* (Curran), by Goeden et al. (1995) and Goeden (2002), respectively. This paper describes the life history and selected immature stages of a third species, *G. setosa* (Foote).

Materials and Methods

The present study utilized specimens of adults reared from 1-liter samples of mature flower heads of *Ericameria brachylepis* (A. Gray) H. M. Hall collected at a single location in southern California: South of Banner along Chariot Canyon Road at 980-m elevation in northeastern San Diego County. The life history study and description of the immature stages of *G. setosa* were based in large part on dissections of samples of live, immature and mature, flower heads and dead, overwintered flower heads collected during 1995–1999. One-liter samples of these flower heads containing the scarce larvae and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Sixteen third-instar larvae and nine puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbent cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, studied and digitally photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

A few adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C and 14/10 (L/D) photoperiod. A virgin male and female obtained from emergence cages were held in a clear-plastic, petri dish provisioned with a flattened, water-moistened pad of absorbent cotton spotted with honey (Headrick and Goeden 1994) for observations of courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001a, b, c; 2002), Goeden et al. (1993), Goeden and Headrick (1992), Goeden and Norrbom (2001), Goeden and Teerink (1997), Headrick et al. (1996), Teerink and Goeden (1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Digitized photographs used to construct text figures were processed with Adobe Photoshop® Version 6.

Results and Discussion

Taxonomy

Adult.—*Goedenia setosa* was described by R. H. Foote (in Blanc and Foote 1987) in the genus *Urophora* based on a single male collected from Tar Canyon, Kings County, California. Freidberg and Norrbom (1999) reclassified most of the indigenous, western North American species of *Urophora* as *Goedenia*. A wing photograph of *G. setosa* was provided by Blanc and Foote (1987) and Foote et al. (1993), and the head was figured in dorsal view in Foote et al. (1993).

Foote et al. (1993) noted that "most" *G. setosa* and "most" *G. timberlakei*, along with *Neomyopites* (as *Urophora*) *claripennis* (Foote) are the only U.S. and Canadian *Myopitini* with an entirely black scutellum. Two males (9%) of 22 adults of *G. setosa* reared from flower heads at the study site had the middle third of the scutellum yellow; the scutella of the remaining flies were entirely black. Similarly, 60 (20%) of 302

adults of *G. timberlakei* reared from 11 different hosts (Goeden 1987, unpublished data; Goeden et al. 1995) had the apex of the scutellum ocherous to bright yellow instead of all black.

Immature stages.—*Third instar larva:* Elongate-ellipsoidal, roundly tapered anteriorly, bluntly truncated posteriorly (Fig. 1A), integument white, but venters of meso-, metathorax, and abdominal segments A1–A4 with dark brown to black infuscation; caudal segment, including spiracles, dark brown or black; minute acanthae conical, bluntly or sharply pointed (Figs. 1B-1, E-1), or hemispheroidal (Figs. 2A-1, C-1), and outwardly or posteriorly directed, circumscribe anterior fifth and all of venters of meso- and metathorax, and all but middle half of abdominal segment A1, including all of venters, circumscribe all of A2–A7, and cover dorsal half and posterior part of caudal segment; prothorax smooth, but venter with flattened, pointed, posteriorly directed minute acanthae (Figs. 1B-1, C-1), and circumscribed by verruciform sensilla medially (Fig. 1B-2); gnathocephalon conical and medially divided by a vertical cleft (Fig. 1C-2), pore (Fig. 1D-1) above each dorsal sensory organ; dorsal sensory organ well-defined, hemispherical (Figs. 1D-2); anterior sensory lobe (Figs. 1C-3, D-3) bears terminal sensory organ (Fig. 1D-4), lateral sensory organ (Fig. 1D-5), supralateral sensory organ (Fig. 1D-6), and pit sensory organ (Fig. 1D-7); two medial, papilliform integumental petals (Fig. 1D-8), five, lateral, spatulate or papilliform, integumental petals (Fig. 1D-9) above each mouthhook (Fig. 1C-4), lateralmost integumental petal (Fig. 1D-10) separate from stomal sense organ (Figs. 1C-5, D-11) ventrolaterad of anterior sensory lobe; mouthhook bidentate (Fig. 1C-4); median oral lobe laterally compressed, apically pointed (Fig. 1C-6); verruciform sensilla circumscribe gnathocephalon dorsolaterally, laterally, and ventrolaterally (Figs. 1C-7, D-12); anterior thoracic spiracle on posterior margin of prothorax bears two doliform papillae

(Figs. 1B-3, E-2, F-1); mesothoracic, lateral spiracular complex with five verruciform sensilla in vertical series (Fig. 1F-2), mesothoracic spiracle not seen; metathoracic lateral spiracular complex with nearly closed, lateral spiracle (Figs. 1F-3, 2A-2) on posterior margin of anterior, circumnatal band of minute acanthae (Fig. 2A-1); five verruciform sensilla (Figs. 1F-4, 2A-3) in a vertical series posterior to lateral metathoracic spiracle; lateral spiracular complex of abdominal segment A1 consists of a nearly closed spiracle (Figs. 1F-5) and three verruciform sensilla in vertical series posterior to spiracle (Fig. 1F-6); caudal segment with pair of posterior spiracular plates (Fig. 2B-1) surrounded by hemispherical minute acanthae (Figs. 2B-2, C-1) interspersed dorsally, medially, and less so, ventromedially with open pores (Figs. 2B-3, C-2), these structures in turn ringed by two to three, concentric series of shallow, elliptical depressions (Fig. 2B-4), with verruciform sensilla dorsolaterally, laterally, and ventrolaterally outside these depressions (Fig. 2B-5); two, tapered stelex sensilla (Figs. 2B-6, C-3, D) and another verruciform sensillum (Figs. 2B-7, C-4, E) also dorsolateral to each posterior spiracular plate; posterior spiracular plate bears three, smoothly flattened, elliptical rimae (Fig. 2F-1), ca. 0.02 mm in length, and four, spinose, interspiracular processes, each ca. 0.005 mm long (Fig. 2F-2).

The habitus of the third instar of *G. setosa* resembles that of *G. timberlakei* (Goeden et al. 1995) and *G. rufipes* (Goeden 2002). In all three species, the venter of the thorax and the caudal segment are darkly pigmented (Fig. 4B, Goeden et al. 1995, Goeden 2002) and minute acanthae circumscribe the meso- and metathorax and abdomen, and especially noteworthy, the central, posterior surface of the caudal segment, which also is prominently dotted with scattered pores (Figs. 4D-3, E-3; Goeden et al. 1995). However, in *G. setosa* the minute acanthae and pores appear less numerous and more centralized (Figs. 4D-3, E-3) than
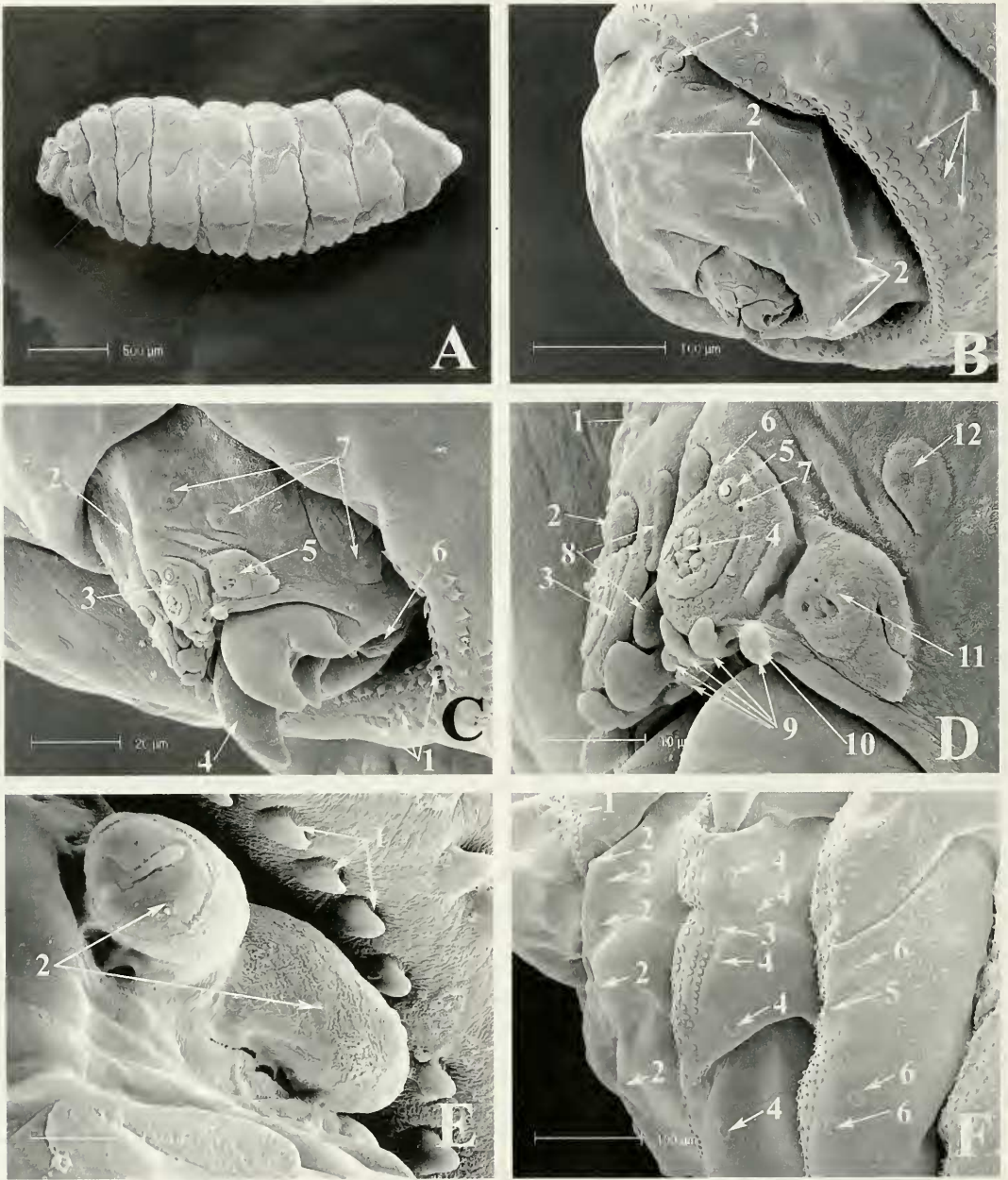
Fig. 1.   Third instar of *Goedenia setosa*: (A) habitus, anterior to left; (B) gnathocephalon and prothorax, frontolateral view, 1—minute acanthae, 2—verruciform sensilla, 3—anterior spiracle; (C) gnathocephalon, frontolateral view, 1—minute acanthae, 2—vertical, medial cleft, 3—anterior sensory lobe, 4—mouthhook, 5—stomal sense organ, 6—median oral lobe, 7—verruciform sensilla; (D) gnathocephalon, close-up, 1—pore, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—terminal sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ, 7—pit sensory organ, 8—medial integumental petals, 9—lateral integumental petals, 10—lateralmost integumental petal, 11—stomal sense organ, 12—verruciform sensillum; (E) anterior spiracle, 1—minute acanthae, 2—papillae; (F) lateral spiracular complexes, 1—anterior spiracle, 2—verruciform sensilla on mesothorax, 3—lateral spiracle on mesothorax, 4—verruciform sensilla on metathorax, 5—spiracle on first abdominal segment, 6—verruciform sensilla on first abdominal segment.
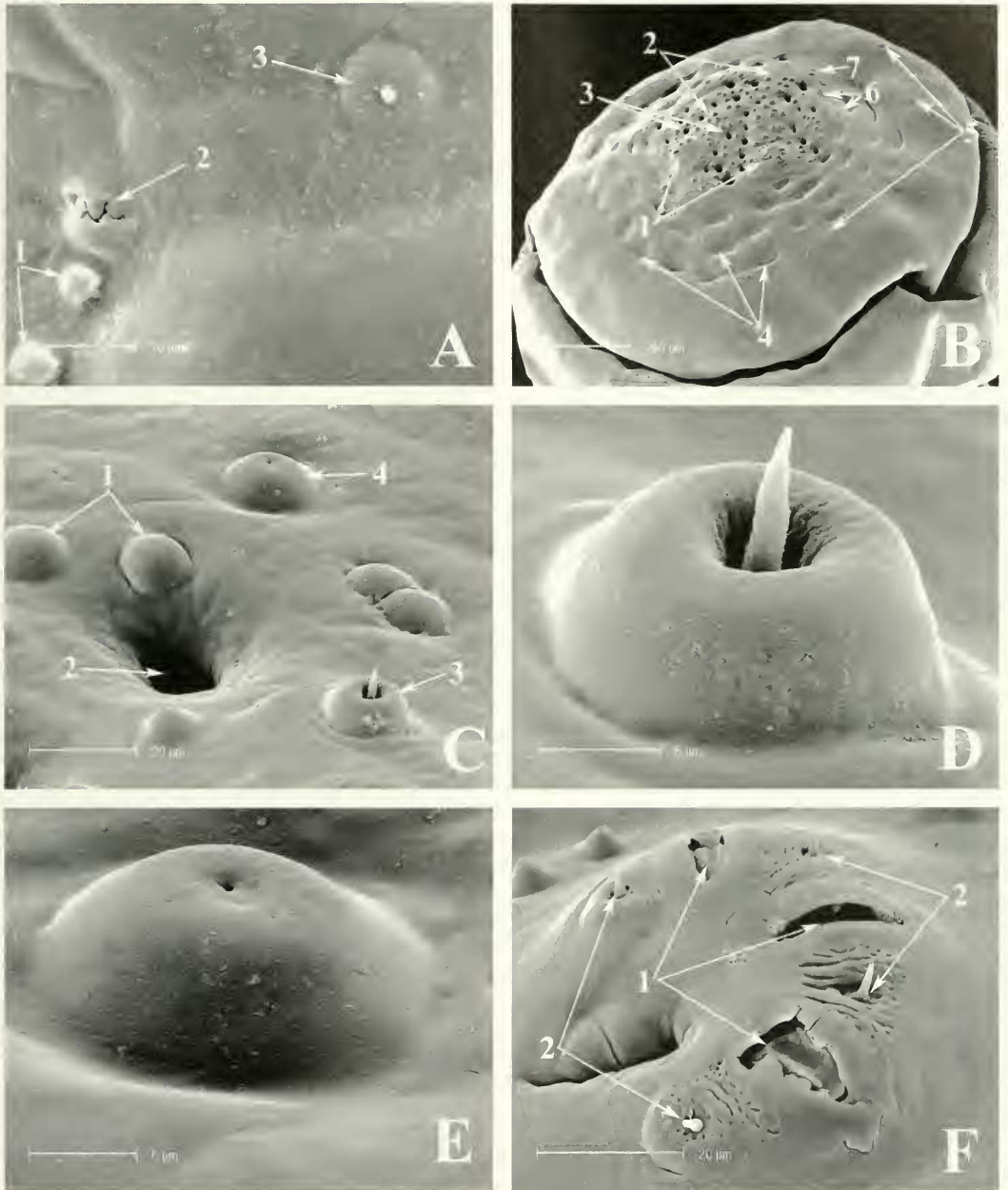
Fig. 2. Third instar of *Goedenia setosa*, continued, (A) close-up of lateral spiracular complex of metathorax, 1—minute acanthae, 2—spiracle, 3—verruciform sensillum; (B) caudal segment, 1—posterior spiracular plates, 2—minute acanthae, 3—pores, 4—shallow, elliptical depressions, 5—verruciform sensilla, 6—stelex sensilla, 7—verruciform sensillum; (C) close-up of caudal segment, 1—minute acanthae, 2—pore, 3—stelex sensillum, 4—verruciform sensillum; (D) stelex sensillum, (E) verruciform sensillum, (F) posterior spiracular plate, 1—rimae, 2—interspiracular processes.

in *G. timberlakei* (Goeden et al. 1995, unpublished data) and *G. rufipes* (Goeden 2002), and in *G. setosa* also are replaced peripherally by concentric series of shallow, elliptical depressions (Fig. 2B-4). Because *G. setosa* also exhibits shallow depressions (Fig. 2B-4) surrounding the center of the caudal segment, what I have termed pores may instead be deep depressions.

The prothorax and gnathocephalon of *G. timberlakei* and *G. rufipes* are smooth and free of minute acanthae (Goeden et al. 1995, Goeden 2002); whereas, the prothoracic venter of *G. setosa* anteriorly bears minute acanthae (Figs. 1B-1, C-1). Two medial and five lateral integumental petals are present in *G. setosa* (Figs 1D-8, -9); whereas, *G. timberlakei* has two medial and six lateral integumental petals (Goeden 2002). The lateralmost of these lateral integumental petals is separated from the stomal sense organ in all three species (Figs. 1C-4, D-10; Goeden et al. 1995, Goeden 2002).

The third instars of the three species of *Goedenia* studied to date lack oral ridges on either side of the mouth opening, and ventral or ventrolateral to the stomal sense organ (Figs. 1C, D; Goeden et al. 1995, 2002a, unpublished data).

The mouthhooks of the third instars of *G. setosa* (Fig. 1C-6), like those of *G. timberlakei* (Goeden et al. 1995) and *G. rufipes* (Goeden 2002), are bidentate; however, a vertical view of the oral cavity like that figured for *G. rufipes* (Goeden 2002) was not obtained for either *G. timberlakei* (Goeden et al. 1995, unpublished data) nor *G. setosa*. Thus, the concave, posterior surface of the anterior tooth described for *G. rufipes* could not be compared with the other two species.

The lateral spiracular complex of the mesothorax of *G. setosa* includes five verruciform sensilla in a vertical series (Fig. 1F-2); whereas, in *G. timberlakei*, this same complex includes only two verruciform sensilla (Goeden et al. 1995), but six such sensilla in *G. rufipes* (Goeden 2002).

The anterior spiracle of all three species

bears only two papillae (Figs. 1E-2, F-1; Goeden et al. 1995, Goeden 2002).

The metathoracic lateral spiracular complex of *G. setosa* includes five verruciform sensilla (Fig. 1F-5, 2A-3), but again, only two such sensilla in *G. timberlakei* (Goeden et al. 1995) and four such sensilla in *G. rufipes* (Goeden 2002). Finally, three verruciform sensilla comprise the lateral spiracular complex of the first abdominal segment of *G. setosa* (Fig. 1F-7) and *G. rufipes* (Goeden 2002), but only one verruciform sensillum is found on this segment in *G. timberlakei* (Goeden et al. 1995).

Puparia: Light to dark, reddish brown with dark brown to black, anterior stripe on venter of meso- and metathorax and abdominal segments A1–A4, and similarly dark caudal segment, elongate-ellipsoidal, with smoothly rounded anterior end and truncated posterior end (Fig. 3A). Anterior end bears invagination scar (Fig. 3B-1) and raised, bilobed, anterior thoracic spiracles (Fig. 3B-2). Flattened posterior end of caudal segment studded with smoothly rounded, hemispherical, minute acanthae (Fig 3C-1) interspersed with open pores (Fig. 3C-2). A pair of raised, hemispheroidal, posterior spiracular plates (Fig. 3C-3) each bear three elliptical rimae interspersed with four, peg-like, interspiracular processes. These structures are ringed by shallow, elliptical depressions (Fig. 3C-4). Thirty-two puparia dissected from flower heads of *Ericameria brachylepis* averaged 2.68 ± 0.02 (range, 2.42–2.85) mm in length; 1.10 ± 0.02 (range, 0.94–1.28) mm in width.

DISTRIBUTION AND HOSTS

To date, *Goedenia setosa* only is reported from two locations in southern California (Blanc and Foote 1987), i.e., the type locality and the Chariot Canyon study site, and from its newly reported, sole known host plant, *Ericameria brachylepis*. Like all other known hosts of *Goedenia* spp. (Goeden 1987, Foote et al. 1993), *E. brachylepis* belongs to the family Asteraceae, tribe Astereae, and subtribe Solidagininae (Bremer
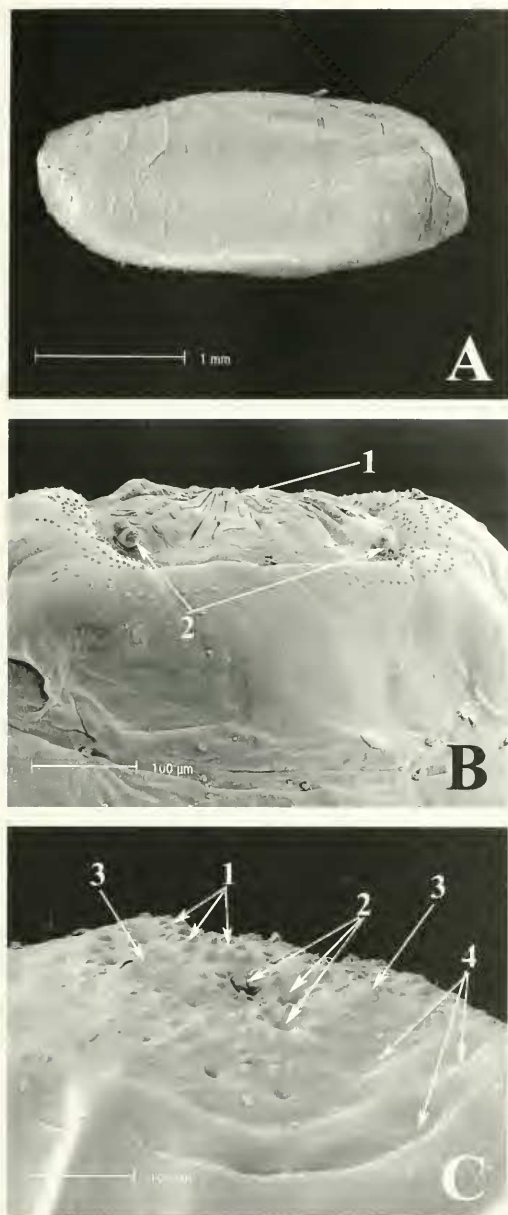
Fig. 3. Puparium of *Goedenia setosa:* (A) habitus, anterior to right, (B) anterior end, 1—invagination scar, 2—anterior spiracles; (C) caudal segment, 1—minute acanthae, 2—pores, 3—posterior spiracular plates, 4—shallow, elliptical depressions.

1994). Accordingly, *G. setosa* apparently is a monophagous, or nearly monophagous, tephritid. The distribution of *E. brachylepis* includes the southern Peninsular Ranges and South Coast of California [regions de-

liniated in Hickman (1993)] and northern Baja California, Mexico, below 1500 m (Hickman 1993). As the type locality lies outside this distribution, it is possible that another, as-yet-to-be-determined, alternate host plant exists for *G. setosa* in southern California, which if so, probably also belongs to the genus *Ericameria.*

BIOLOGY

Because *G. setosa* co-occurred with *Trupanea wheeleri* Curran and *Neospilota viridescens* Quisenberry in separate flower heads of *E. brachylepis* at the Chariot Canyon study site ("symphagy", Goeden 1997), where *G. setosa* was much less common than the former tephritids, flower heads containing eggs and first instars of *G. setosa* could not be distinguished or described.

Larva.—Upon eclosion, the first instar presumably tunneled immediately through the inner bracts and into an ovule of a pre-blossom flower head like *G. rufipes* (Goeden 2001a). There, it fed with its body perpendicular to and its mouthparts toward the receptacle within an ovule, which it first excavated, then exited and entered an adjacent ovule. The receptacle was neither abraded or pitted by such feeding.

An average of 1.2 ± 0.2 (range, 1–2) second instars was found feeding on ovules in six, separate, closed, preblossom flower heads (Fig. 4A). They usually fed within an ovule with their bodies perpendicular to, but always above, the receptacles (Fig. 4A). Receptacles of the six flower heads containing second instars averaged 0.95 ± 0.05 (range, 0.85–1.14) mm in diameter. These larvae had damaged an average of 3.7 ± 1.0 (range, 1–7) ovules, or about 46% of the average total of 8.0 ± 0.6 (range, 6–10) ovules counted within each of the six flower heads. However, more than 1,200 flower heads were individually dissected in order to locate these six flower heads infested with second instars.

Third instars fed with their long axes oriented perpendicular to the receptacles, and
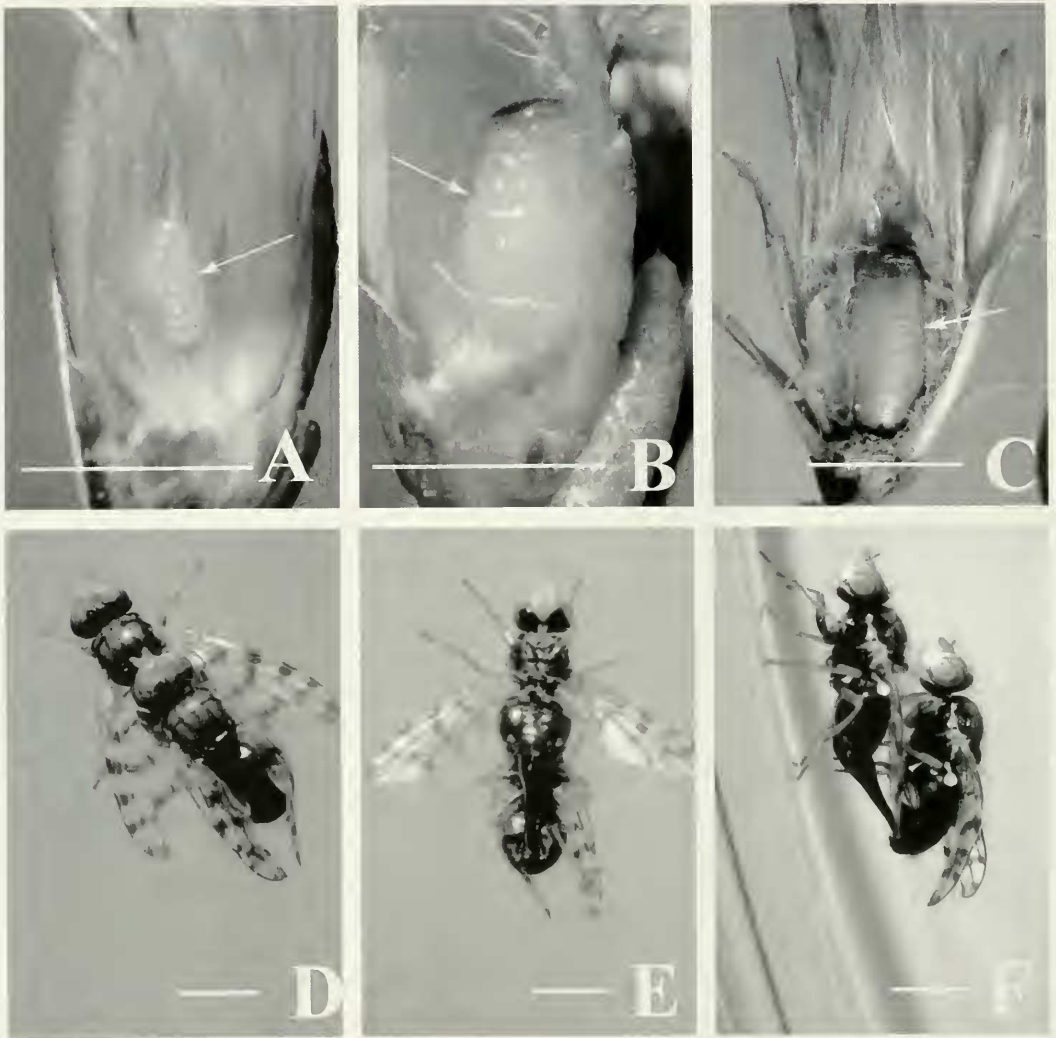
Fig. 4. Life stages of *Goedenia setosa* in flower heads of *Ericameia bachylepis:* (A) second instar (arrow) feeding on floret; (B) third instar (arrow) feeding on soft achenes and receptacle in flower head; (C) puparium in flower head (arrow); (D) mating pair, dorsal view; (E) mating pair, ventral view; (F) mating pair, lateral view. Lines = 1 mm.

with their mouthparts directed towards the receptacles, which they scored or pitted deeply in 11 (44%) of 25 flower heads examined (Fig. 4B). The 25 flower heads (eight, closed preblossom; five, open blossom; 12 postblossom) were dissected and contained an average of 1.0 ± 0.04 (range, 1-2) third instars. These 25 flower heads averaged 1.01 ± 0.03 (range, 0.85–1.42) mm in diameter and contained an average total of 8.6 ± 0.4 (range, 6-10) ovules/achenes,

of which on average 6.9 ± 0.8 (range, 2–10) ovules/achenes were damaged or about 80% (Fig. 4B). Again, well over 1,000 flower heads were individually dissected to locate these 25 infested flower heads.

The receptacles that were pitted (Fig. 4B) suggested that sap constituted at least part of the diet of third instars of *G. setosa*. Goeden (1988), Headrick and Goeden (1990), Goeden and Headrick (1992), Goeden et al. (1993, 1995), Headrick et al. (1996), Goe-

den and Teerink (1997) first noted, described, and discussed sap feeding by florivorous species of Tephritidae in the genera *Trupanea, Paracantha, Neaspilota, Tephritis, Goedenia* (as *Urophora*), *Dioxyna,* and *Xenochaeta,* respectively. Sap could also be transported to the feeding larvae through the corniculae attaching the basal fragments of the ovules/soft achenes to the receptacle. Upon completing feeding, the larva constructed a vasiform cell consisting of ovule/achene/floret fragments impregnated with and hardened by dried, liquid feces and sap. The inside wall of this cell was smooth and ringed by buried pappus fragments, reflecting the turning motions of the larva during the construction of the apically open-mouthed cell. The flattened, sclerotized caudal segment apparently serves as a plug that tightly closes the mouth of the cell, yet allows respiration, and thus also may help to shield the third instar from natural enemies, especially predators. Prior to pupariation the prepupa turns 180° and orients with its anterior end away from the receptacle, retracts its mouthparts, and forms a puparium (Figs. 4C).

Pupa.—The receptacles of 29 flower heads each containing a single puparium (Figs. 4C) averaged 1.12 ± 0.02 (range, 1.10–1.14) mm in diameter. The posterior of the puparium faced the receptacle, rested in the cuplike base of the cell, but free of the inner wall of the cell (Fig. 4C).

Adult.—Under insectary conditions, eight males of *G. setosa* lived an average of 49 ± 3 (range, 36–61) days, and two females lived for 41 and 75 days. These longevities were slightly longer than the mean longevities reported for *G. timberlakei* (Goeden et al. 1995), but fully commensurate with the aggregative type of life histories of both tephritids (Headrick and Goeden 1994, 1998; Goeden et al. 1995).

The premating and mating behaviors of *G. setosa* were not studied in the field, but were observed for a male and female paired when 1-day old in a petri dish arena of the type found to be useful with many other nonfrugivorous, tephritid species (Headrick and Goeden 1994). Both sexes exhibited wing hamation (Headrick and Goeden 1994) throughout the day concurrent with other behaviors, i.e., grooming, resting, and feeding; this also was the most common wing movement reported for *G. timberlakei* (Goeden et al. 1995) and *G. rufipes* (Goeden 2002). Premating behaviors observed with *G. setosa* included males and females tracking individuals of the opposite sex, during which males sometimes swayed and usually exhibited abdominal pleural distension. During mating, the wings of the male were parted at about 20°, the wings of the female were parted at 60–70°, with both pairs of wings centered over the midlines of the files (Figs. 4D, E). The foretarsi of the male grasped the female abdomen dorsolaterally at the thoracic juncture, the midtarsi grasped the oviscape at its base, and the hindtarsi crossed under the oviscape or rested on the substrate (Fig. 4F). During copulation, the body of the female was parallel to the substrate with the oviscape raised about 20°, while the extended aculeus pushed the male upward and backward at an angle of about 20° anteriorly (Fig. 4F). This pair was observed to mate once or twice per day, on several successive days during a 41-day period, for a total of 21 matings that lasted an average of 158 (range, 30–320) min. The female evidenced restlessness before termination of mating by pushing against the male with its hind tarsi, by lofting its wings so as to push them against the male, and by fully extending its aculeus. The male in turn countered this behavior with copulatory induction behavior (CIB), rocked from side to side to regain purchase or to avoid the female's pummeling, and sometimes rapidly vibrated his wings, all of which appeared to calm the female and allow coitus to continue. During separation the male turned and rapidly walked off and away from the female while pulling his genitalia free, a process lasting about 5 s (n = 2).

Seasonal history.—The life cycle of *G.*

setosa in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the prepuparia and puparia, and some adults variously are the overwintering stages. Adults emerge from a few puparia formed in late-fall (October–November) and these unmated, sexually immature adults overwinter. The remaining prepuparia, and puparia overwinter in dead flower heads on dormant *Ericameria brachylepis*. These overwintered individuals emerge as adults in late winter (February–March) and pass the following spring and summer (April–August), probably as non-reproductive individuals in riparian habitats. They eventually aggregate on preblossom, fall-blooming, *E. brachylepis*, mate, and subsequently oviposit in the small, newly-formed, closed, preblossom flower heads.

Natural enemies.—Overwintered puparia of *G. setosa* were heavily parasitized and yielded a variety of chalcidoid, primary parasitic Hymenoptera, i.e., *Colotrechnus* sp. (Eulophidae), *Eurytoma* sp. (Eurytomidae), *Eupelmus* sp. (Eupelmidae), *Halticoptera* sp. (Pteromalidae), and *Mesopolobus* sp. (Pteromalidae).

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